

## REVIEW OF THE *CASTILLEJA PURPUREA* COMPLEX (OROBANCHACEAE)

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### ABSTRACT

Since 1958, the purple-bracted *Castilleja purpurea* has been treated to include the yellow-bracted *C. citrina* (as *C. purpurea* var. *citrina*) and the red- to orange-bracted *C. lindheimeri* (as *C. purpurea* var. *lindheimeri*). It is proposed here that each of the three be treated at specific rank, emphasizing their largely consistent morphology, the relatively narrow zones of hybridization along areas of contact, compared to the much larger areas within which each of the three is consistent, and the consistent distinction between *C. citrina* and *C. purpurea* even within a significant area of sympatry. *Castilleja purpurea* and *C. citrina* in the northern part of their ranges (Kansas, Oklahoma, Missouri) are allopatric, while in central Texas they are sympatric. The region of sympatry is characterized by a mix of populations of typical morphology and populations of variable bract and calyx color — sympatric populations of *C. citrina* are considerably less variable than any of *C. purpurea*. *Castilleja lindheimeri* is parapatric to narrowly sympatric with both *C. purpurea* and *C. citrina* and morphologically distinct from both, although some hybrids occur. A biologically appropriate taxonomy of most populations of the *C. purpurea* complex is possible with identifications of *C. purpurea*, *C. citrina*, and *C. lindheimeri*, for intergrades using *C. purpurea*< >*citrina*, *C. purpurea*< >*lindheimeri*, and *C. lindheimeri*< >*citrina*, or simply "*C. purpurea* complex intergrade."

*Castilleja purpurea* (Nutt.) G. Don and *C. lindheimeri* A. Gray were early described from collections of early explorers. After traveling and observing in Texas, Pennell (1935) added *C. citrina* Pennell as well as two other Texas paintbrush species he considered to be narrow endemics. Lloyd Shinnars moved to Texas in 1945, and after becoming familiar with the flora of central Texas, probably upon seeing variable populations in north-central counties, he reckoned that the whole *C. purpurea* complex was best conceptualized as a single species (1958). His nomenclatural combinations were not accompanied by any explanatory comment. Since the precedent by Shinnars, floristic accounts and studies have followed in recognizing *C. purpurea* with three varieties (e.g., Holmgren 1970; Great Plains Flora Association 1986; Nesom 1992; Diggs et al. 1999; Turner et al. 2003; Nelson 2009).

In 2013, with the advantage of having a large number of collections at hand to study, with personal paintbrush experience in the field by both authors, and with the opportunity to review the *Castilleja purpurea* complex in connection with preparation of the FNA *Castilleja* treatment, we offer an alternative point of view. Many questions arise in relation to whatever taxonomic approach is taken, and we hope that the underlying biology of these plants will become better understood. The hypothesis guiding the nomenclature presented here can be tested in various ways.

Observations pertinent to the taxonomic interpretation follow below, with a formal presentation of the nomenclature. The distribution map (Fig. 1), which summarizes information

critical to our interpretation, is derived mostly from specimens examined at TEX-LL, BRIT-SMU-VDB, BAYLU, TAES-TAMU, NLU, and MO. All photos are by Egger.

### Typical forms and variants

Over most of their geographic ranges, and even in areas of sympatry, *Castilleja citrina* (yellow inflorescence; Figs. 4, 6, 7), *C. purpurea* (purple inflorescence; Figs. 2, 3), and *C. lindheimeri* (red inflorescence; Figs. 10, 11) occur in populations of relatively narrow variation in bract and calyx color. Color differences among the three imply that isolating mechanisms may involve differences in pollinators. Introgression appears to be limited in geographical extent, but widely variable populations are conspicuous and occur mostly along zones where ranges are in close contact (Fig. 1). Populational variants from pinkish purple to red, reddish orange, burnt orange, pink, peach, light yellow, creamy (very light orange-yellow), and rarely white have been observed.

*Castilleja citrina* and *C. purpurea* are allopatric in Kansas and most of Oklahoma, but they are partially sympatric in north-central Texas and into southeastern Oklahoma. Typical populations of purple-bracted *C. purpurea* exist in the area of sympatry, and many sympatric populations of *C. citrina* also are consistent in morphology, the plants identifiable by their yellow bracts and calyces and large, yellow, thin-petaloid lower corolla lips. Some observations suggest that gene flow is mostly unidirectional from *Castilleja citrina* into *C. purpurea*. "Populations of [*C. citrina*] are considerably less variable in coloration than in the other two [taxa]. ... Genes of [*C. citrina*] apparently are present in populations of [*C. purpurea*] in their region of contact, but not vice versa, as if [*C. citrina*] were serving only as the pollen parent of the putative hybrids" (Nesom 1992, p. 216–217).

*Castilleja citrina* and *C. lindheimeri* are parapatric or narrowly sympatric in south-central Texas counties (Fig. 1), mostly away from the range of *C. purpurea*, and little evidence of intergradation between them is evident in herbarium collections. Hybridization probably does occur, however, as indicated by an orangish yellow plant from Gillespie County (Fig. 9), where only *C. citrina* and *C. lindheimeri* occur.

*Castilleja lindheimeri* and *C. purpurea* are parapatric or narrowly sympatric (Fig. 1). Each apparently maintains a consistent morphology except immediately along the area of contact (e.g., in Coleman Co., Fig. 5). A set of vouchers was made from a population "between highway [317] and railway" in McLennan County (4 Apr 1949, *Cory* 55470 a, b, c, d, e, and f, SMU), where only *C. lindheimeri* and *C. purpurea* occur, with the label observation that the population included six color forms (all apparently mostly red to pink or purplish).

Pennell (1935) cited as *Castilleja lindheimeri* a few collections from counties within the geographic range of *C. purpurea* but outside that of *C. lindheimeri* (e.g., Comanche, Eastland, Erath, Menard, Mills, Parker, Stephens). This probably reflects the difficulty in determining color of calyces and bracts in specimens that were not dried quickly in preparation or with color faded in age. Recent collections, especially those where inflorescence color is noted in the collection data, support the distinction in geography between *C. lindheimeri* and *C. purpurea*, as mapped in Figure 1.

### One species or three?

The three entities of the *Castilleja purpurea* complex are differentiated mostly in the color of bracts and calyces. Putative differences in corolla and calyx sizes noted by Pennell (1931) do not appear to be consistent. The distinctively large, petaloid, lower corolla lip of *C. citrina* noted by Pennell and others is generally consistent and diagnostic, but lips of similar morphology (except in color) sometimes also occur in *C. purpurea*.



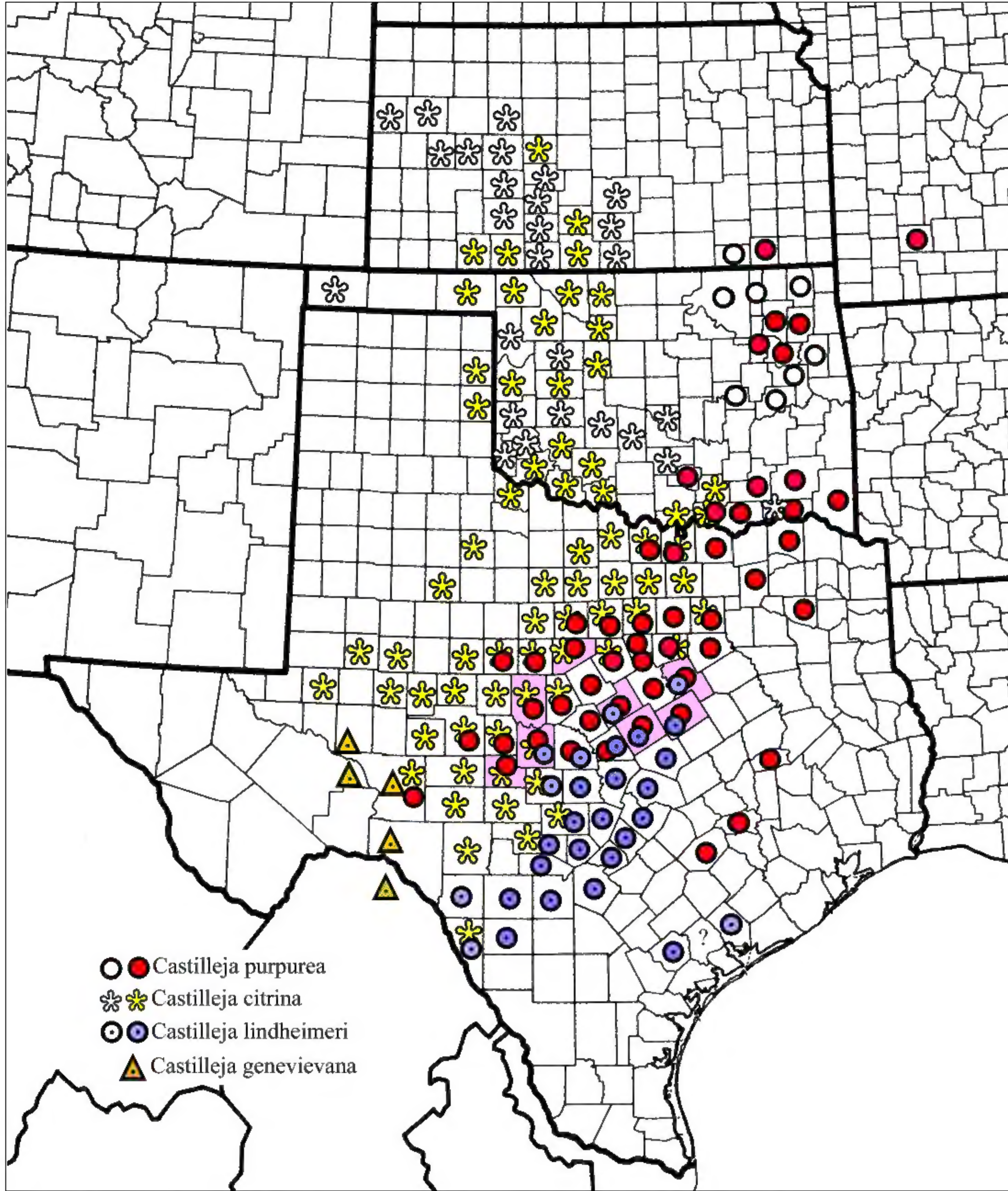


Figure 1. Distribution of the *Castilleja purpurea* complex and the yellow-bracted *C. genevievana*. Counties with pink background are those in which populations widely variable in bract and calyx color are known to occur. Uncolored symbols are from OVPD (2012) and BONAP (2013). Texas county records added from Pennell (1935): *C. lindheimeri* – Jackson; *C. purpurea* – Fayette. The record from Greene Co., Missouri is this: Percy Cave, Apr 1903, *P.C. Standley s.n.* (US, photo MO!).



The morphological consistency (aside from color) and geographic coherence of this complex indicates that these three entities comprise a closely related group, probably arisen from a single ancestor (see potential caveat below regarding *Castilleja citrina*). Rare yellow color variants within *C. purpurea* far-removed from *C. citrina* populations, and color variants within *C. citrina* and *C. lindheimeri*, perhaps reflect an ancestral gene pool. This and the variability of populations at contact zones have formed the rationale for treating them within a single species.

The alternative proposed here, recognition of three separate species, emphasizes their largely consistent morphology, the relatively narrow zones of hybridization along areas of contact, compared to the much larger areas within which each of the three is consistent, and the consistent distinction between *Castilleja citrina* and *C. purpurea* even within a significant area of sympatry. A somewhat analogous situation exists between the widespread *C. miniata* Douglas ex Hook. and the primarily Rocky Mountain species *C. rhexiifolia* Rydb. (Holmgren 1984). If broader zones of hybridization and introgression existed among the entities, their recognition as varieties within a single species would seem more appropriate.

The taxonomic interpretation is subjective, depending upon the underlying species concept — no formal definition exists regarding how strictly isolating mechanisms must limit hybridization and/or introgression in order to justify the recognition of distinct species. Subjectivity in the instance at hand may extend further, since evidence in support of one or the other interpretation might be regarded as equivocal. It does seem likely, however, that treating the entities at specific rank will have greater effect in evoking further study.

Hybridization among these taxa and the conspicuousness of populational variability probably greatly increased as road corridors were developed. Pennell himself in 1920, presumably before exceptionally wide rights-of way became characteristic of Texas roadways, made collections of *Castilleja* in Texas (in Bexar, Coleman, Hays, Kendall, Kerr, Randall, Tom Green, and Travis counties, as cited in the 1935 study, mostly in the ranges of *C. citrina* and *C. lindheimeri*), but he did not mention highly variable populations in his 1935 study. In fact, he noted specifically (p. 531) that *C. lindheimeri* "is not so variable in color as Gray supposed."

#### Hybridization between the *Castilleja purpurea* complex and other species

Interspecific hybridization is common in *Castilleja* (Egger 1994) and taxonomic implications of its occurrence must be interpreted in context. Pertinent to the present situation, hybrids and hybrid swarms between *C. purpurea* and *C. indivisa* Engelm. are observed where they are sympatric. Figure 12 shows such a hybrid at a locality where both species in typical expression were growing (McCulloch Co., Egger 851, WTU). At one site in Coryell Co., Texas, intermediates and apparent backcrosses toward both parents produced a wide range of combinations of morphological features, including bract and calyx color, corolla, calyx, and leaf morphology, habit, and even duration (judging from the root development) (Nesom 7279–7283, TEX; Nesom 1992). Similar interactions between these two species have been observed at other Texas localities (e.g., Bosque Co., McBryde 3022, SMU; Wise Co., Swadek 156, BRIT), though in at least some other mixed populations hybrids are rare and likely first generation (e.g., Hill Co., Egger s.n., WTU). In the latter population, two apparent hybrids were collected for chromosomal analysis and proved to have irregularities, including anomalous chromosome numbers of  $n = 14$  and  $n = 16$  in a genus with a base number of  $x = 12$ . Hybrids also occur between *C. indivisa* and *C. lindheimeri* (e.g., Hays Co., Nesom 7283, TEX) and *C. indivisa* and *C. citrina* (e.g., Clay Co., Burgard 115, BAYLU; Travis Co., Clary s.n., BRIT, TEX). *Castilleja indivisa* is probably most closely related to *C. coccinea* (L.) Spreng. of the eastern USA, *C. scorzonifolia* Kunth widespread in Mexico, and *C. rigida* Eastw. of trans-Pecos Texas and north-central Mexico, and *C. purpurea* and *C. indivisa* would never be considered conspecific, based on their propensity to hybridize.

The putative hybrids between *Castilleja citrina* and *C. indivisa* in Travis Co. (SW side of Austin, 14 Apr 1992, *Clary s.n.*) apparently are sterile, as the ovaries are unexpanded even in the oldest, withered flowers and no seeds are formed. The label notes that there was a "small population of yellow-bracted plants mixed with *C. indivisa*. Intermediates apparently not present." The yellow-bracted plants have lobed leaves and bracts but the bracts are unusually broad and the inflorescence uncharacteristically loose for *C. citrina*.

The geographic ranges of *Castilleja citrina* and *C. genevievana* Nesom (Fig. 8) approach each other in southwest Texas (Fig. 1) but do not become contiguous. The latter is mostly entire-leaved, but with lobed bracts, and probably is closely related to the red-bracted *C. integra* A. Gray, but it would be interesting to know whether these two closely geographically associated yellow-bracted species are independently evolved or whether their yellow display might reflect shared ancestry. If the latter, the case for treating *C. citrina* at specific rank would be strengthened.

### Taxonomy of the *Castilleja purpurea* complex

- 1. Bract and calyx apices yellow, less commonly orangish yellow ..... **Castilleja citrina**
- 1. Bract and calyx apices mostly shades of red, purple, and pink, rarely yellowish or white.
  - 2. Bract and calyx apices predominantly purple to pinkish purple, varying to red, reddish orange, burnt orange, peach, light yellow, creamy, and rarely white (albino) ..... **Castilleja purpurea**
  - 2. Bract and calyx apices red to reddish orange or orange ..... **Castilleja lindheimeri**

**CASTILLEJA CITRINA** Pennell, Proc. Acad. Nat. Sci. Philadelphia 73(3C): 532. 1922. *Castilleja purpurea* var. *citrina* (Pennell) Shinnery, Spring Fl. Dallas-Ft. Worth, 410. 1958. **TYPE:** USA. Texas. Coleman Co.: Talpa, stony limestone knoll, 20 May 1920, *F.W. Pennell 10516* (holotype: NY!; isotypes: DS!, GH!, K! digital image!, MO! digital image!, OKLA!, PH!, TEX! digital image!, US!).

*Castilleja labiata* Pennell, Proc. Acad. Nat. Sci. Philad. 73(3C): 530. 1921[1922]. **TYPE:** USA. Texas. Tom Green Co.: San Angelo, stony prairie, uncommon, 19 May 1899 *W.L. Bray 353* (holotype: US! digital image!; isotype: TEX! digital image!).

Bract and calyx apices yellow (sometimes described as chrome yellow or lemon yellow), less commonly orangish yellow. Figures 4, 6, 7.

Flowering (Mar–)Apr–May. Calcareous prairies, sandy fields, gravelly limestone hillsides, limestone outcrops, roadsides, mesquite, juniper, oak-juniper, and post oak woodlands; 300–800 m; Kans., Okl., Tex.

**CASTILLEJA PURPUREA** (Nutt.) G. Don, Gen. Syst. Gard. Bot. 4: 615. 1838. *Euchroma purpurea* Nutt., Trans. Amer. Philos. Soc., n.s. 5(6[2]):180. 1837[1835]. **TYPE:** USA. **Oklahoma.** [probably Choctaw Co.]: "On rocks in the hilly prairies of Red river," May 1819, *T. Nuttall s.n.* (holotype: BM! digital image!; isotypes: K-HOOK(2)! digital image!, PH!).

Nuttall collected in present-day eastern Oklahoma in the summer of 1819 (Nuttall 1821; Lawson 2004). In late May through the first half of June, he explored and botanized along the Kiamichi River, mostly in present day Choctaw, Pushmataha, and LeFlore counties, to its mouth at the Red River.

*Castilleja purpurea* (Nutt.) G. Don f. *corallina* Waterf., Rhodora 56: 160, 1954. **TYPE:** USA. **Oklahoma.** Choctaw Co.: Prairies on "blackland" (shallow limestone-derived soil), 0.5 mi N of the junction of Hwys 271 and 70, NW of Hugo, 15 Apr 1950, *U.T. Waterfall 9287* (holotype: OKLA!; isotype: GH!).

*Castilleja* × *williamsii* Pennell [pro species], Acad. Nat. Sci. Philadelphia Monogr. 1: 530. 1935. **TYPE:** USA. Texas. Goliad Co.: Goliad, Apr 1927, *Rev. C.B. Williams 116* (holotype: PH!;



isotype: TEX! digital image!). Pennell cited these as paratypes: Washington Co.: Brenham, *Hobart s.n.* (GH); without locality, *Drummond 286* (GH).

Bract and calyx apices predominantly purple to pinkish purple, varying to red, reddish orange, orange, peach, light yellow, creamy, and rarely white (albino forms). Many other phrases are used to describe the colors, especially in variable populations, e.g., purplish red, rose, scarlet rose, purplish rose, burnt orange, lavender pink, cerise pink. Figures 2, 3.

Flowering (Mar–)Apr–May. Calcareous prairies, rocky fields, rocky limestone roadbanks, hills, and ledges, calcareous and sandy roadsides, sandy hillsides, juniper, juniper-oak, and post oak woodlands, post oak-hackberry thickets; 250–600 m; Kans., Mo., Okl., Tex.

The type of *Castilleja williamsii*, from Washington Co., Texas, has entire leaves but the bracts are trifid, the bracts and calyces are purplish, and the thick, woody roots indicate that it is perennial. *Williams 115* (PH, TEX!), apparently collected from near the type of *C. williamsii* (*Williams 116*, perhaps the same population), has lobed leaves and was cited by Pennell (p. 530) among the "specimens examined" for *C. purpurea*. A more recent collection from Washington County (3 Apr 1990, *Jones 4167*, VDB) is identified here as typical *C. purpurea*. The plants of *Williams 116* perhaps are *C. purpurea* with genetic influence from *C. indivisa* and are appropriately identified as *C. x williamsii*.

Entire leaves also occur elsewhere in *Castilleja lindheimeri*, e.g., Travis Co. (*Albers s.n.*, SMU; *Carr 4629*, BRIT; *Jones 4273*, VDB; *McCart 6693*, SMU) – in these, leaves on the proximal 2/3 of the stem are entire while those distal are lobed. Entire leaves in *C. citrina*, similarly mostly proximal cauline, also occur in Kansas, e.g. Clark Co. (*Brooks 14695*, VDB), Meade Co. (*Freeman 10556*, VDB) and probably in Texas and Oklahoma as well.

**CASTILLEJA LINDHEIMERI** A. Gray, *Syn. Fl. N. Amer.* 2(1): 298. 1878. *Castilleja purpurea* var. *lindheimeri* (A. Gray) Shinnars, *Spring Fl. Dallas-Ft. Worth*, 410. 1958. TYPE: USA. Texas. [Gillespie Co.] Pierdenales, mountain prairies on somewhat moist places, Apr 1847, *F. Lindheimer 385*, *Flora Texana Exsiccata* 669 (holotype: GH digital image!; isotypes: MO 4 sheets!). The specimen was annotated by Gray as *Castilleja lindheimeri* and noted by Pennell in 1930 as the "TYPE" and mistakenly by Egger in 1996 as the holotype. Protologue: "Stony or fertile mountain prairies, on the Pierdenales and Guadalupe, W. Texas, Lindheimer, &c." *Castilleja mearnsii* Pennell, *Acad. Nat. Sci. Philadelphia Monogr.* 1: 530. 1935. TYPE: USA. Texas. Kinney Co.: Ft. Clark, 15 Mar 1893, *E.A. Mearns 1291* (holotype: US! digital image!; isotype: PH!).

Bract and calyx apices red to reddish orange or orange. Figures 10, 11.

Flowering Mar–May. Pastures, grassland, calcareous and sandy roadsides, rocky limestone roadbanks, slopes, and ridges, among granite boulders, juniper, oak-juniper, and live oak woodlands; 300–800 m; Tex.

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Figure 2. *Castilleja purpurea* in typical form. Ca. 5 miles east of Santa Anna, along U.S. Hwy 67, Coleman Co., Texas, 20 Apr 1997.





Figure 3. *Castilleja purpurea* in typical form. Ca. 3 miles east of Bangs, Brown Co., Texas, 20 Apr 1997.





Figure 4. *Castilleja citrina* in typical form, with immediately adjacent plants of *C. purpurea* perhaps with influence of *C. citrina*. Figure 5 shows another view of the same population. Ca. 3 miles east of Talpa, Coleman Co., Texas, 20 Apr 1990. Talpa is the type locality for *C. citrina*.



Figure 5. Variable population, including forms apparently intermediate between *C. citrina* and *C. purpurea*. Ca. 3 miles east of Talpa, Coleman Co., Texas, 20 Apr 1990. *Castilleja citrina* in typical form occurs at this site (Fig. 4). Coleman County is slightly northwest of the known range of *C. lindheimeri*, but the brick red colored plants suggest that its influence also may be showing here.





Figure 6 *Castilleja citrina* population in typical form East of Ballinger, Runnels Co., Texas, 6 Apr 1997





Figure 7. *Castilleja citrina* in typical form. West of Benoit, Runnels Co., Texas, 20 Apr 1997.



Figure 8. *Castilleja genevievana*. East of Sheffield, Crockett Co., Texas, 19 Apr 1997. Does the yellow color indicate shared ancestry with *C. citrina*?





Figure 9. *Castilleja citrina*, orangish yellow, perhaps reflecting influence of *C. lindheimeri* in an area where the two are parapatric or narrowly sympatric. West of Fredricksburg, Gillespie Co., Texas, 3 Apr 1990.





Figure 10. *Castilleja lindheimeri* in typical form. Cypress Creek Park, northwest of Austin, Travis Co., Texas, 3 Apr 1990.





Figure 11. *Castilleja lindheimeri* in typical form. West of Lometa, Lampasas Co., Texas, 20 Apr 1997.





Figure 12. *Castilleja indivisa* x *C. purpurea*, presumed F1 hybrid (right) with typical *C. indivisa* (left), ca. 3 miles east of Brady, McCulloch Co., Texas, 20 Apr 1997. In the hybrid plant, note the deeply divided leaves and relatively longer corolla beaks of *C. purpurea* and the largely emarginate calyxes of *C. indivisa*, along with the more or less intermediate coloration of the bracts and calyxes. The bracts are red like *C. indivisa*, the purple of *C. purpurea* apparently not expressed even in intermediacy.